

Hydrodynamic synchronization of autonomously oscillating optically trapped particles

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Ellipsoidal micron-sized colloidal particles can oscillate spontaneously when trapped in a focused laser beam. If two oscillating particles are held in proximity their oscillations synchronize through hydrodynamic interactions. The degree of synchronization depends on the distance between the oscillators and on their orientation. Due to the anisotropic nature of hydrodynamic coupling the synchronization is strongest when particles are arranged along the direction of oscillations. Similar behavior is observed for many oscillating particles arranged in a row. Experimental observations are well reproduced with a model that uses a phenomenological description of the optical force and hydrodynamic interactions. Our results show that oscillating ellipsoidal particles can serve as a model system for studying hydrodynamic synchronization between biological cilia.

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Synchronization appears at all length scales from atoms to macroscopic bodies and is ubiquitous in living systems [1]. For example at microscale it plays an important role in the motion of microswimmers such as protozoa [2], algae [3] or spermatozoa [4] which use flagella or cilia for their propulsion. A green alga *Chlamydomonas* swims with two flagella which it moves in a coordinated way reminiscent of a human doing the breaststroke. The coordination of flagella is crucial for swimming along a straight line [3]. Ciliates like *Paramecium* coordinate the beating of their cilia to form metachronal waves which greatly enhance their swimming efficiency [5]. Similar waves are also observed in cilia that cover respiratory epithelia and clear mucus from the airways [6]. Hydrodynamic synchronization can even be observed between flagella of two separate sperm cells swimming beside each other [4]. In large numbers hydrodynamically synchronized spermatozoa can form intriguing vortex patterns [7]. The formation of metachronal waves has been recreated in an artificial system consisting of microtubule bundles and kinesin motors [8].

Synchronization of nearby swimming microorganisms with waving tails was first studied by G. Taylor who showed that it can lead to a reduced dissipation [9]. However, this finding does not explain the kinematic mechanism that keeps the tails synchronized. A difficulty lies in the temporal reversibility of the Stokesian hydrodynamics while synchronization is irreversible by nature [10]. This can be overcome either by breaking the temporal symmetry in the driving mechanism [11, 12] or by describing a cilium with more than one degree of freedom [13]. In addition, synchronization can also result from indirect coupling between cilia caused by a rocking motion of the cell body [14, 15], or from inertial effects at

non-zero Reynolds number [16].

Hydrodynamic synchronization was studied in model system containing spherical colloidal particles actively driven along closely spaced circular trajectories via feedback controlled optical tweezers [17–21]. Cicuta and co-workers demonstrated an in-phase and anti-phase synchronization where the transition between the two modes was controlled by changing the shape of the driving potential [19]. In all these experiments the driving mechanism required video particle tracking and computer controlled feedback.

Alternatively hydrodynamic synchronization can be studied in a system of optically trapped non-spherical particles. A recent study reported synchronous rotation of two particles in vortex beams [22]. Elongated particles in a focused beam can also exert oscillatory motion [23, 24]. Their oscillations are induced by a combination of the gradient force that pulls the particle towards the beam center and a non-conservative force due to the radiation pressure. In this Letter we report on experiments in which such oscillating ellipsoidal particles were exploited to study the hydrodynamic synchronization between two or more closely spaced autonomous oscillators.

Experiment. Ellipsoidal prism shaped particles (Fig. 1a) were fabricated from a layer of photoresist (SU-8, MicroChemicals) by maskless photo-lithography using direct laser structuring (LPKF ProtoLaserD) [25]. Particles were dispersed in water and sealed in a thick sample cell. The experiment was conducted on a setup built around an inverted microscope (Zeiss Axiovert) equipped with a multi-trap laser tweezers system (Aresis Tweez) using 1064 nm IR laser (Coherent Compass) and high numerical aperture water immersion objective (Zeiss Achromat 63×0.9 NA) [26]. Kinematic information on particle motion was obtained from video recordings captured with a CMOS camera (Pixelink PL-B 741) and subsequently analyzed by proprietary particle tracking software [27]. At the beginning of each measurement one or multiple particles sedimented at the bottom of the experimental cell were trapped and pushed against the upper cell wall.

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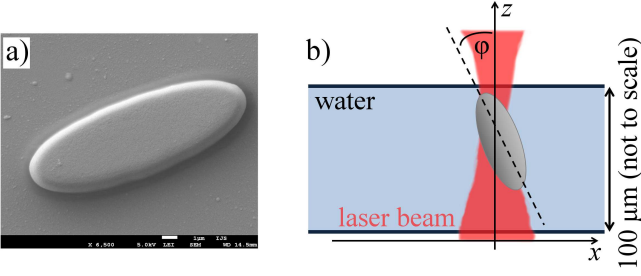


FIG. 1: a) SEM image of a particle with major radius $8\mu\text{m}$, minor radius $2.5\mu\text{m}$ and thickness $2.2\mu\text{m}$. b) φ denotes the angle between the particle's long axis and the z -axis, x the distance between its center of reaction and the center of the laser beam.

In order to control the orientation of a particle each trap consisted of a principal beam and a secondary beam with 20% of the main beam's power that was shifted against the main beam by $2\mu\text{m}$ perpendicular to the x -axis.

Single particle oscillations. Once a trapped particle is pushed against the upper cell wall (Fig. 1b) it reaches a steady state in which it persistently oscillates about the center of the trapping laser beam. The oscillations take place in a plane orthogonal to the flat surface of the particle. Figure 2a shows a time series of images demonstrating the oscillatory motion. The position of the particle center as a function of time is shown in Fig. 2b. Since all optical forces are proportional to the light intensity we expected and found a linear dependence of the oscillation frequency on the laser power (Fig. 2c).

The dynamics of an ellipsoidal particle in the optical tweezers beam can be described as follows. If we define the particle position as its center of reaction [28] its mobility tensor becomes diagonal (a force causes no rotation and a torque no translation) and the equations of motion are

$$\dot{x} = M_{TT}F, \quad \dot{\varphi} = M_{RR}T \quad (1)$$

where φ is the angle between the particle's long axis and the z -axis and x the distance between the center of reaction and the axis of the laser beam (Fig. 1b). We propose the following expressions for the force and the torque acting on the particle

$$\begin{aligned} F &= -Ax + B\varphi \\ T &= -Cx + D\varphi - E\varphi^3. \end{aligned} \quad (2)$$

The coefficient A describes the restoring potential of the laser trap, B is the effect of tilt – the radiation pressure on a tilted particle exerts a lateral force; C is the restoring torque of the trap boundary; D describes the torque on a particle pressed against a wall that causes an instability and E is a restoring torque that counteracts the instability. The equations of motion (1) can then be

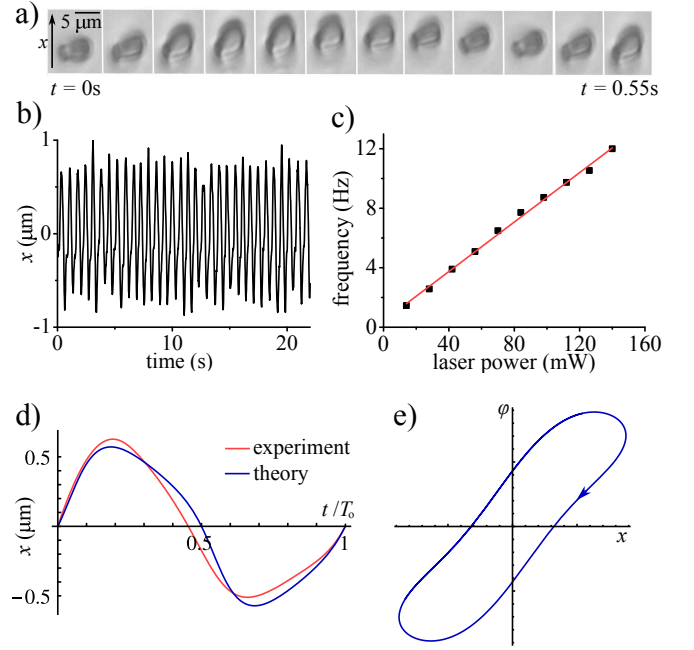


FIG. 2: a) Time sequence of an oscillatory motion of an ellipsoidal particle trapped by laser beam. b) Dynamics of the oscillating particle in y direction. c) Particle's oscillation frequency as a function of laser power. The solid line represents a linear fit to the data. d) Oscillatory period of an ellipsoidal particle comparing the experimental and theoretical data for $\alpha = 0.8$ and $\beta = 1.5$. e) Stable limit cycle for same values of α and β as in d).

written in the form

$$\begin{aligned} \dot{x} &= \Omega(-\alpha x + \epsilon\varphi) \\ \dot{\varphi} &= \Omega\left(-\frac{1}{\epsilon}x + \beta\varphi - \delta\varphi^3\right). \end{aligned} \quad (3)$$

Of the five parameters Ω determines the oscillation frequency, δ the amplitude and ϵ the amplitude ratio between x and φ . The dynamical behavior of the system is governed by the two essential parameters (α and β). The dynamical system described by Eq. 3 always has a fixed point at $(0,0)$ and for $\alpha\beta > 1$ it has two more at $\pm\sqrt{(\alpha\beta - 1)/(\alpha\delta)}(\epsilon/\alpha, 1)$. The fixed point at $(0,0)$ is stable if $\alpha > \beta$ and $\alpha\beta < 1$. At $\alpha = \beta$ it undergoes a Hopf bifurcation and becomes unstable, encircled by a limit cycle. At $\alpha\beta = 1$ there is a pitchfork bifurcation (transition from 1 to 3 fixed points) and for $\alpha\beta > 1$ $(0,0)$ becomes a saddle point. The remaining two fixed points are stable if $\alpha + 2\beta - 3/\alpha > 0$ and unstable otherwise. The latter transition is a subcritical Hopf bifurcation. The dynamical regimes of the system are shown in Fig. 3.

Figure 2d shows a measured oscillation cycle obtained by averaging the experimentally obtained particle position as a function of time over many periods. The shape of this oscillation cycle is visibly asymmetric and compares well to the trajectories obtained from model equations in the region with 3 fixed points. Equations of mo-

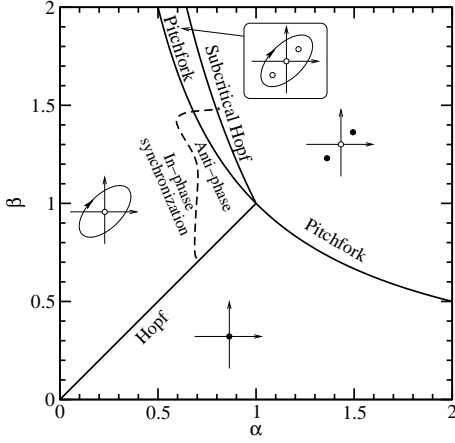


FIG. 3: Bifurcation diagram for a single particle described by Eqs. 3. Depending on the parameters α and β , the model can exhibit one or three fixed points and a limit cycle that describes autonomous oscillations. In addition, the diagram shows (dashed line) the regions in which two particles show in-phase and anti-phase synchronization for parameter values corresponding to longitudinal arrangement at large distances ($c_{RR}/c_{TT} = 0.5$, $c_{TR}/(\epsilon c_{TT}) = 0.5$, $c_{RT}\epsilon/c_{TT} = 1.5$).

tion (3) were solved numerically for $\alpha = 0.8$ and $\beta = 1.5$. The limit cycle of the oscillator for the same parameters is shown in Fig. 2e. From this comparison we conclude that an oscillating particle can be adequately described by the phenomenological model we introduced here. Furthermore, it has been demonstrated that an oscillator with two degrees of freedom is a good candidate for hydrodynamic synchronization in [13].

Two particle synchronization. To study hydrodynamically mediated synchronization between independent oscillators we trapped two ellipsoidal particles in separate beams and brought them in close proximity. Measurements were performed for three different alignments of the particles with respect to the direction of oscillation: longitudinal (inset Fig. 4b), diagonal (Fig. 4c) and lateral alignment (Fig. 4d). An example of particle positions vs. time is shown in Fig. 4a for an interparticle distance of $8\mu\text{m}$ (half the particle size) and longitudinal configuration. Synchronized oscillation is clearly visible.

The degree of synchronization can be visualized in a scatter plot of particle positions x_1 vs. x_2 (Fig. 4b-d). For an interparticle distance of $15\mu\text{m}$ the graph shows a strongly correlated motion for longitudinal alignment (Fig. 4b) indicating that oscillating particles synchronized in-phase. For diagonal alignment the motion is still synchronous although the correlation is weaker (Fig. 4c). For the lateral alignment the motion is not correlated showing that the oscillations are out of synchrony (Fig. 4d). This observation is in accordance with the anisotropy of Oseen's tensor which is even more pronounced in the presence of a no-slip boundary [29]. We quantitatively evaluate the degree of synchrony by calculating the Pearson correlation coefficient as a function

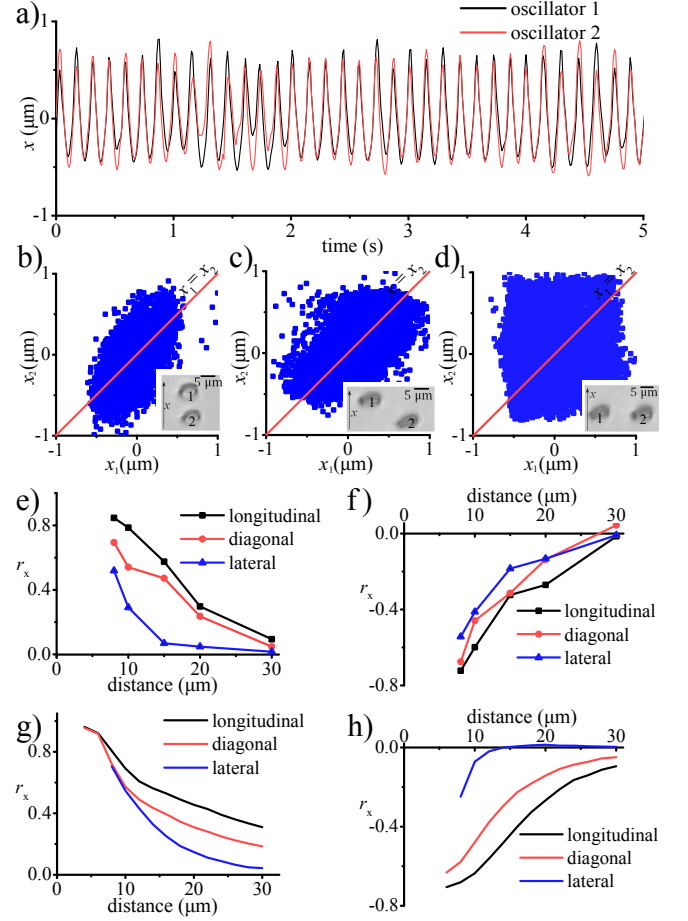


FIG. 4: a) Position oscillations of two particles in longitudinal arrangement (inset in b)) at a distance of $8\mu\text{m}$, laser power 56 mW. b)-d) Synchronization strength at distance $15\mu\text{m}$ for three arrangements: b) longitudinal, c) diagonal, d) lateral. The insets show the position of the particles. Laser power: 56 mW. e)-f) Correlation coefficient r_x as a function of the interparticle distance d for different arrangements showing (e) in-phase synchronization (laser power 28 mW) and (f) anti-phase synchronization (laser power 42 mW). g)-h) Theoretically calculated correlation coefficients with parameters $\alpha = 0.8$, $\beta = 1.5$, $\epsilon = 14\mu\text{m}$ (g) and $\epsilon = 6\mu\text{m}$ (h).

of interparticle distance (Fig. 4e). In one instance the particles also showed robust antiphase synchronization (Fig. 4f). The type of synchronization was largely invariant of the laser power. We conclude that the transition from in-phase to anti-phase synchronization was governed by the detailed properties of the laser beam in the vicinity of the surface.

To understand the hydrodynamic synchronization we extend the phenomenological model (3) by taking into account the fluid-mediated interaction. The force or torque which sets one particle and the surrounding fluid in motion also has an effect on the velocity and angular velocity of the second particle. Their equations of motion can be

written as

$$\begin{aligned}\dot{x}_{1,2} &= M_{TT}F_{1,2} + C_{TT}F_{2,1} + C_{TR}T_{2,1} \\ \dot{\varphi}_{1,2} &= M_{RR}T_{1,2} + C_{RT}F_{2,1} + C_{RR}T_{2,1}\end{aligned}\quad (4)$$

where x_i and φ_i denote the deflection of i -th ($i = 1, 2$) particle, F_i the force and T_i the torque acting on it. C_{TT} , C_{TR} , ... denote the coupling coefficients (off-diagonal elements of the two-particle grand mobility matrix). By introducing the reduced coefficients $c_{TT} = C_{TT}/M_{TT}$, $c_{RR} = C_{RR}/M_{RR}$, $c_{TR} = C_{TR}/M_{RR}$, $c_{RT} = C_{RT}/M_{TT}$ and inserting F and T from Eq. 2 we obtain

$$\begin{aligned}\dot{x}_1 &= \Omega_1(-\alpha x_1 + \epsilon \varphi_1) + c_{TT}\Omega_2(-\alpha x_2 + \epsilon \varphi_2) \\ &\quad + c_{TR}\Omega_2(-\frac{1}{\epsilon}x_2 + \beta \varphi_2 - \delta \varphi_2^3) \\ \dot{\varphi}_1 &= \Omega_1(-\frac{1}{\epsilon}x_1 + \beta \varphi_1 - \delta \varphi_1^3) + c_{RT}\Omega_2(-\alpha x_2 + \epsilon \varphi_2) \\ &\quad + c_{RR}\Omega_2(-\frac{1}{\epsilon}x_2 + \beta \varphi_2 - \delta \varphi_2^3)\end{aligned}\quad (5)$$

for particle 1 and analogous equations for particle 2. In this expression we assumed that the two oscillators differ only in their characteristic frequencies (Ω_1 and Ω_2). A numerical solution of the equations of motion (5) for two identical oscillators ($\Omega_1 = \Omega_2$) reveals that if the particles are only coupled through the c_{TT} coefficient, they will synchronize in anti-phase except for a narrow region with small α . The coefficients c_{RR} and c_{RT} always lead to in-phase synchronization and c_{TR} always to anti-phase. As a consequence, the nature of synchronization will depend sensitively on the ratio between coupling coefficients.

We determined the coupling coefficients numerically by modeling the particles as ellipsoids orthogonal to a wall. We solved the hydrodynamic problem with a boundary element method (BEM) by representing each particle with 512 elements and incorporating the no-slip boundary condition at the plate into the Green function [30] (Fig. S1). We assumed a distance between the particle tip and the wall of $0.1 \mu\text{m}$ and checked that the choice of this value only has a minor influence on the calculated coefficients. In the calculation we restricted the motion to the direction along the x -axis in which active oscillations take place. The resulting coupling coefficients are shown in Fig. S2. In order to reproduce a realistic situation we simulated two oscillators with a frequency mismatch $\Omega_2/\Omega_1 = 1.2$ (based on the measured average frequency difference between particles that are out of range of hydrodynamics interactions) and additional noise. The resulting correlation coefficients are shown in Fig. 4g. They show qualitative agreement with the measured values under similar conditions, both in their distance- and direction-dependence. Frequency mismatch and noise both contribute to the loss of synchrony at larger distances. The relative weight of different coupling coefficients c_{TT} etc. depends sensitively on the parameter ϵ . A small variation can lead to a regime where the two oscillators show anti-phase synchronization (Fig. 4h). As

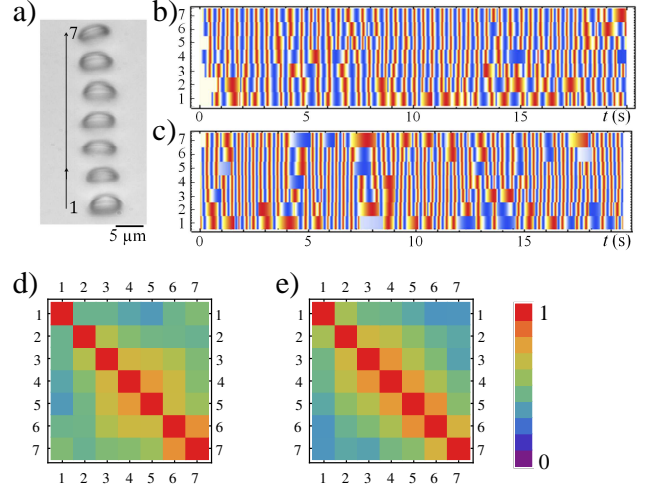


FIG. 5: a) Particles arranged in a row. b) Phase profile: laser power 40 mW per particle and distance between adjacent particles 8-9 μm . c) Simulation of the same system using parameters $\alpha = 0.8$, $\beta = 1.5$, $\epsilon = 12 \mu\text{m}$. d) Correlation matrix of experimentally measured particle positions. e) Equivalent correlation matrix from simulation.

one can see from the phase diagram for typical parameters (Fig. 3, dashed line) the parameter range that allows anti-phase synchronization is rather narrow. This provides a possible explanation for the rare instances in which anti-phase synchronization was observed in the experiment.

Synchronization in particle row. Following the two-particle experiments we investigated if hydrodynamic interactions can also lead to synchronization in a row of particles. When biological cilia are densely covering a surface their oscillations usually form metachronal waves whose direction and wavelength vary from system to system. A problem that arises in theoretical models of wave formation is that the cilia at the ends of a chain are subject to different interactions with their neighbors than those in the middle. As a consequence some models obtain synchronization or metachronal waves when they introduce periodic boundary conditions but not in a finite chain [31], although the latter is possible, too [32]. Likewise, experimental studies on model systems concentrated on particles arranged in closed ring structures [18].

In our experiment 7 optical traps were arranged in a linear row with a spacing of $8 \mu\text{m}$ (Fig. 5a). Particles never showed complete synchrony or phase waves. Figure 5b shows an example where a high degree of local synchrony persisted over many oscillations but not indefinitely. The correlations are stronger in the middle of the chain and weaker at its ends (Fig. 5d).

We also extended the theoretical model to a row of particles. We used the same parameters as for two particles and applied the distance-dependent coupling coefficients (Fig. S2) to describe the interaction between a particle and all other particles in the chain. A phase plot

of a simulated system with the same parameters we used for two particles is shown in Fig. 5c and the correlation matrix between all oscillators in Fig. 5e. Like in the experiment partial order but no complete synchronization can be seen. The loss of synchrony is mainly due to geometric effects in the chain, because the particles at the end are subject to weaker interactions than those in the middle.

In conclusion, we have shown that elliptical colloidal particles oscillating in a laser beam provide a good model system for studying hydrodynamic synchronization. In a two-particle system we showed that the coupling strength depends on the interparticle distance as well as their spatial arrangement. While particles usually synchronize in-phase, anti-phase synchronization was observed as well. For many particles arranged in a row we observe

only weak synchronization in agreement with theoretical results. A question that remains to be investigated is whether 2-dimensional arrays of oscillators would show more robust synchronization and what are the necessary conditions for the formation of metachronal waves in such a system.

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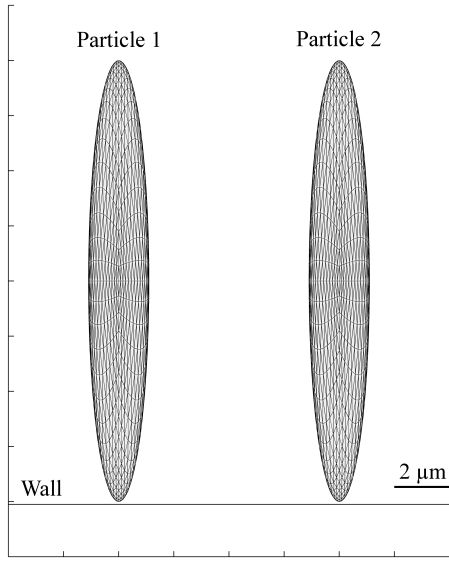


FIG. S1: Boundary element representation of two ellipsoidal particles (side view) in close proximity to a wall with no-slip boundary condition.

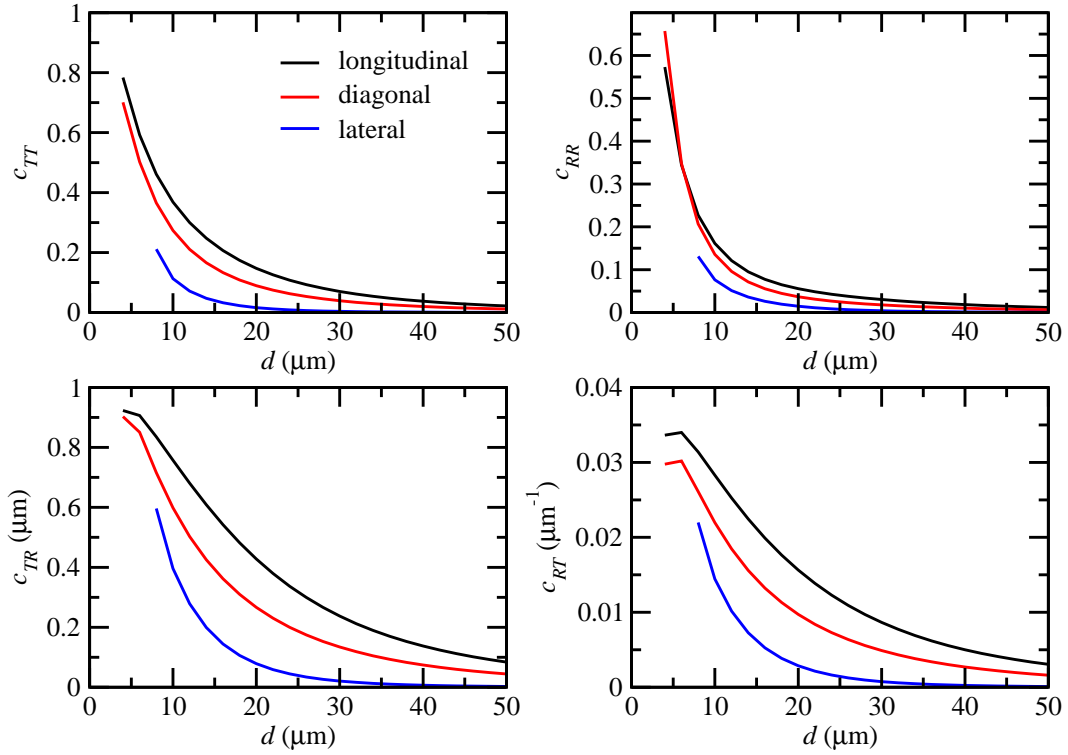


FIG. S2: Reduced coupling coefficients c_{TT} , c_{RR} , c_{TR} , c_{RT} calculated with the boundary element method (BEM) as a function of interparticle distance d for longitudinal, diagonal and lateral spatial arrangement.